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ABSTRACT

We compared published results of the age-at-maturity and relative fecundity of female sablefish *Anoplopoma fimbria* sampled just prior to the spawning season nearby Kodiak Island in 2011 to results from a study in the same geographic area in 2015. The rate of skip-spawning was higher in 2011 (21%) than in 2015 (6%) and, therefore, in 2011 there were larger effects on the estimates of age-at-maturity when skip-spawning fish were classified as mature or immature than in 2015. When skip-spawning fish were classified as mature, the age-at-50% maturity in 2011 was 0.5 years younger than in 2015. When skip-spawning fish were classified as immature, age-at-50% maturity was 1.9 years older in 2011 than in 2015. Generally, skip-spawning was at ages where a portion of the fish were not yet mature (i.e., the age at which fish were estimated to be <100% mature). For 2011 and 2015 pooled, when including only the age range that included ages where there was skip-spawning, there was a negative relationship between age and skip-spawning, indicating that skip-spawning was more common in younger fish. In addition, relative fecundity by body weight decreased with age (significantly in 2015 and for both years pooled), indicating that as fish age they produce relatively fewer eggs. Although the relationships were diffuse, the estimated decrease in relative fecundity from age 5 to 40 was 21-24%.

CONTENTS

INTRODUCTION

In fisheries stock assessment, female age-at-maturity is integral to estimation of female spawning biomass, which is used to set target biological reference points. The maturity data currently used in the Alaska sablefish stock assessment were collected over 30 years ago and was classified macroscopically using a visual assessment during the summer, which is ~6-9 months prior to spawning (1978-1983; Sasaki 1985). In addition, only lengths were recorded, which were later converted to ages to obtain an age-at-maturity model. The ideal time to sample sablefish for maturity classification and fecundity measurements is just prior to the spawning season and the most accurate method for maturity classification is to examine histology slides microscopically (Hunter et al. 1992).

A recent study of age-at-maturity and fecundity of sablefish in Alaska was conducted in December 2011 in the central Gulf of Alaska (Rodgveller et al. 2016). Skip-spawning female sablefish were observed for the first time, defined as fish that have spawned in the past but would not in the current spawning season. The skip-spawning rate of 21% observed by Rodgveller et al. (2016) had an effect on age-at-maturity curves. When skipped spawning fish were considered mature, the age-at-50% maturity ($a_{50\%}$) was more similar to the value used in the current stock assessment model than when skip-spawning fish were considered immature; when considered immature the curve was shallower and the A_{50} was 3.3 years older (Rodgveller et al. 2016). Skip-spawning rates are dramatically different among species, ranging from 9% to 86% (Secor 2008) and can also be plastic within a stock (Atlantic cod, *Gadus morhua,* Rideout and Rose 2006; Argentine hake, *Merluccius hubbsi,* Macchi et al. 2016). This variation in skip-spawning may have annual effects on age-at-maturity curves. It is important to collect data on skip-spawning from more than one year to determine if rates are consistent.

For many stock assessment population models, including sablefish in Alaska, relative fecundity by weight is assumed to be consistent across ages (Hanselman et al., 2016). Therefore, if there was a change in the relative fecundity by age, the current assumption made in the stock assessment model would lead to a biased estimate of population productivity. This assumption was verified in the 2011 collection; however, those data were collected in a single year.

The objective of this study was to obtain a second estimate of age-at-maturity, skip-spawning rate, and fecundity just prior to spawning for a comparison to data collected in the central Gulf of Alaska (CGOA) in December 2011.

METHODS

Sampling Area

The study area in 2011 and 2015 was located between Kodiak Island and the Kenai Peninsula in the CGOA (Fig. 1), which is the approximate center of the Alaska sablefish population (Hanselman et al. 2016). In both years the commercial trawl vessel, the F/V *Goldrush*, was chartered to conduct fishing operations. Sampling occurred from 12 to 21 December 2011 (Rodgveller et al. 2016) and 3 to 10 December 2015.

Fish Sampling

In 2011, maturity samples were taken based on a length-stratified sampling design (Rodgveller at al. 2016). In 2015, all female sablefish caught were sampled. In both years, each specimen had its length recorded (cm), was weighed (g), and the sagittal otoliths were removed for ageing. Ovaries were preserved in 10% formalin in 2011 and in 2015 a portion of ovaries were preserved in 10% formalin and a portion in Excel Plus ™. The fixatives change the rate of water loss in the tissue, but the use of different fixatives should not affect the appearance of ovarian structures in histology slides. Otoliths were aged by personnel of the Alaska Fisheries Science Center (AFSC) Age and Growth Program using the standard validated ageing methods (Fargo and Chilton 1987, Kimura and Anderl 2005, Kimura et al. 2007).

Maturity Classification

Ovaries were thin-sectioned, mounted on glass slides, and stained with hematoxylin and counterstained with eosin for an evaluation of microscopic structures and classifying maturity. Maturity was classified based on the most advanced oocyte or structure contained in the ovary as well as other features. Ovaries with the perinucleus (primary growth) oocytes as the most advanced stage were classified as immature. If ovaries had perinucleolar and/or early cortical alveolar oocytes accompanied by evidence of past spawning, which included 1) thick stroma and more space between the lamellae (loose structure with tissue surrounding oocytes), 2) blood vessels within the lamellae, and 3) a thick ovarian wall, they were classified as skip-spawning, as observed in sablefish in December 2011 (Rodgveller et al. 2016). Mature females that were expected to spawn in the current spawning season were characterized by having vitellogenic oocytes. In both years there was no evidence of spawning (i.e., there were no hydrated oocytes, or post-ovulatory follicles).

Fecundity

Fecundity was estimated for a subsample of fish with vitellogenic oocytes. Sablefish have determinate fecundity so the mature cohort of oocytes was clearly separable from immature oocytes based on size and appearance (Mason et al. 1983, Hunter et al 1989, Rodgveller et al. 2016). Fish encompassing a wide range of body lengths were chosen in attempt to incorporate fish with a wide range of ages. Fecundity was measured with the gravimetric method (Murua et al. 2003), where a subsample of oocytes is weighed, the number of oocytes is counted. The number of eggs per gram in the subsample is multiplied by the ovary weight to obtain a total fecundity. Samples were taken from the anterior, middle, and posterior sections and were averaged to estimate total fecundity. The relative fecundity (eggs per gram of body weight/body weight) was calculated for each fish. A linear regression of relative fecundity and age was fit to the annual data separately and for both years combined.

Maturity Models

Female sablefish age-at-maturity was modeled with the logistic function. The two parameter logistic function is given by

$$\hat{p}_a = 1/\left(1 + e^{-\delta(a - a_{50\%})}\right), \qquad (1)$$

where $\hat{p}_a$ is the estimate of the proportion mature at age, δ is the parameter that describes the slope of the logistic (the speed at which maturity approaches 100%), and $a_{50\%}$ is the parameter that describes the age at which 50% of the fish are mature. The observed proportion at age was calculated as

$$p_a = \frac{m_a}{n_a}, \qquad (2)$$

where m_a was the number of mature fish observed at age-a and n_a was the total number of fish at age-a. We used the binomial likelihood to fit the observed proportion mature at age with the logistic model given in equation 1, with an additional penalty when maturity at length or maturity at age-0 was greater than 0%. The penalty function was a weighted least-square between the estimated maturity at age-0 and 0%, given by:

$$P = \lambda(p_0 - 0)^2,$$

where P is the penalty term added to the binomial likelihood, p_0 is the estimated proportion mature at age-0 and λ is the weighting term (selected to be 100 in order to balance fit at age-0 and fit to older ages where maturity is greater than 0%).

Age-at-maturity was estimated for the winter samples in two ways. In the first, fish determined to be skip-spawning were classified as mature and in the second they were classified as immature.

RESULTS

Locations and Sample Sizes

In 2011 fishing occurred on the continental slope and shelf, nearshore bays, and cross-shelf gullies (Fig. 1) (Rodgveller et al. 2016). Due to weather restrictions and the predetermined length stratified sampling methodology, the majority of the sampling in 2011 was restricted to the shelf and nearshore bays (Fig. 1, Table 1) (N = 393), which resulted in a high proportion of samples being young and immature fish. For example, 63% of the samples in 2011 were aged 2–

4, and only 0.8% of these were mature. In 2015, weather allowed for a higher sampling effort in gullies and on the slope, where there were expected to be a higher proportion of fish older than age-2 (sablefish have a pattern of ontogenetic migration from nearshore and more shallow areas to deeper waters on the shelf and slope) (Fig. 1, Table 1) (N = 473). Although no data were collected on the number of males and females encountered, it was noticeable that there were many more males than females in both winter surveys, whereas the ratio was near 1:1 in summer surveys (D. Hanselman, AFSC, pers. comm.).

Prevalence of Skip-spawning

In 2011, 21% of spawning capable fish (N = 23) (those that would spawn or had in the past) were skip-spawning and in 2015 it was only 6% (N = 16) (Table 2). Although there were only seven more fish skip-spawning in 2011 than 2015, there was a lower proportion of spawning capable fish sampled in 2011 than in 2015, resulting in a higher rate of skip-spawning-at-age. All but one skip-spawning fish were ages 4–17 and one was 22 (Table 2). The age range from 4 to 17 generally encompasses the range where a portion of female sablefish are maturing (Rodgveller et al. 2016).

There was a negative, linear relationship between age and the proportion of spawning capable fish skip-spawning when 2011 and 2015 data were combined (Fig. 3). Conversely, there was a positive relationship reported between age and skip-spawning for 2011 data only (Rodgveller et al. 2016). However, for the 2011 analysis, only samples from the shelf were included, because this was where the great majority of the skip-spawning fish were located. Therefore, the data was a measure of the skip-spawning rate in the areas where skip-spawning was more likely to occur. There was no relationship between age and skip-spawning rate for 2015 data only (slope = 0).

Fecundity

For the pooled data and for 2015 alone, there was a significant, negative relationship between relative fecundity and age (P = 0.03 for pooled data; P = 0.09 for 2015) (Table 3). The slopes in both years were similar (Table 3, Fig. 4). There was a 21% decrease in weight-specific fecundity from age-5 to age-40 for pooled data and in 2015 (Table 3). However, the low R^2 and high SEs demonstrate that the relationship between relative fecundity and age is variable and weak.

Age-at-Maturity

The $a_{50\%}$ in 2011 was 9.84 years when skip-spawning fish were considered immature. This estimate is older than estimates from all other models (Table 4, Fig. 5). The $a_{50\%}$ in 2011 was 6.79 years when skip-spawning fish were considered mature. This estimate was more similar to $a_{50\%}$ estimates in 2015; however, the slope of the 2011 curve was steeper than in 2015 so 100% maturity was reached at an earlier age in 2011. The models in 2015 were more similar to one another than the two models in 2011 because the proportion of fish skip-spawning at each age was lower in 2015 than in 2011 (Tables 2 and 4).

The raw proportions were more variable in 2011 when skip-spawning fish were considered both mature and immature (Figs. 6 and 7). This variability resulted in wider 95% confidence intervals in 2011 than in 2015. The variability was most dramatic in 2011 when skip-spawning fish were considered immature (Fig. 7). The 2011 and 2015 curves were more similar to one another when skip-spawning fish were considered mature (Table 4, Fig. 6) than immature (Fig. 7)

DISCUSSION

We found differences in the age-at-maturity and the rate of skip-spawning between 2011 and 2015. Skip-spawning was more prevalent in 2011 and, therefore, the effect of skip-spawning on the age-at-maturity was more dramatic than in 2015. The residuals in the 2011 models were larger than those in 2015, (i.e. the data in 2011 were more dispersed). This was especially true when skip-spawning fish were categorized as immature. This could be attributed to the smaller samples size at most ages in 2011 and/or a real increase in variability in maturity at age in 2011.

As we observed in sablefish, the skip-spawning rate is plastic in other species, such as in Atlantic cod (Rideout and Rose 2006) and Argentine hake (*Merluccius hubbsi*, Macchi et al. 2016). Skip-spawning has been shown to be related to energetic condition, which is related to food quality, availability, and environmental conditions (Burton and Idler, 1987; Rideout and Rose 2006, Skjæraasen et al. 2009, Rideout and Tomkiewicz 2011, Skjæraasen et al., 2012). The environmental conditions in the North Pacific Ocean were in a cool phase starting in 2006 and shifted to a warm, positive Pacific Decadal Oscillation (PDO) phase in fall 2014, resulting in the formation of the warm water “Blob” in the Gulf of Alaska with warm water anomalies continuing through 2016 (Zador 2015, North Pacific Marine Science Organization 2016a). The warm conditions bring less energy-rich copepods, which many taxa depend on directly or indirectly (North Pacific Marine Science Organization 2016b). The warm conditions negatively affect taxa such as squid, crab, shrimp, salmon, birds, and mammals (North Pacific Marine Science Organization 2016b). Conversely, our results from 2015 show that skip-spawning was less prevalent during this warm period. However, most reported measurements and observations are from animals residing or feeding in more shallow water, whereas sablefish less than 2 years old inhabit deep waters from approximately 150 to 1,000 m, where there are few long-term measurements (North Pacific Marine Science Organization 2016b). In addition, it is unknown if changes in productivity and biological diversity closer to the surface may affect animals that reside in deeper water. More data on changes in the benthic environment on the shelf and slope may help to explain variation in sablefish reproduction.

For 2015 and for both years combined, there was an estimated decrease in relative fecundity with increasing age. The R^2 for both models were low and so the model fit may not effectively predict the loss in productivity. Because a departure from a constant relative fecundity may lead to biased estimates of productivity, the relationship between relative fecundity and age should be tracked in the future. Although relative fecundity may decrease with age, we did not study egg quality, which can vary with fish size and age (e.g., Hislop 1988, Carr and Kaufman 2009, Green and Chambers 2007, Sogard et al. 2008). To fully understand the productivity at age, an assessment of relative fecundity and egg quality is needed.

In both years, skip-spawning was most prevalent at ages when fish were maturing and the logistic curve was still approaching 100%. When all data were combined there was a negative relationship between age and skip-spawning. The trend was positive in 2011, however, sample sizes at age were relatively low compared to 2015 so the pooled data may be more reliable. More data are needed to see if there is a trend in the skip-spawning rate by age through time. Like sablefish, skip-spawning in other marine species is more prevalent for younger or smaller (length) fish that have recently matured (e.g., Atlantic cod, Jorgensen et al. 2006, Rideout and Rose 2006; two out of three deepwater *Sebastes*, Conrath et al. 2017). Because skip-spawning is associated with low rations and energy reserves (Burton and Idler 1987, Rideout and Rose 2006, Skjæraasen et al. 2009, Rideout and Tomkiewicz 2011, Skjæraasen et al. 2012), it may be that younger fish are putting a larger proportion of their available energy to growth than older fish, whose growth rate has slowed and, therefore, may have more energy available for reproduction.

There are other models that could be used to describe age-at-maturity when there is a known relationship between skip-spawning and age. We chose to use a 2-parameter logistic model with an asymptote at 100%, where skip-spawning fish were categorized as spawning or immature. There are other potential options for incorporating skip-spawning into maturity models, which may be useful to explore for sablefish if more data on skip-spawning rates at age become available (e.g., Secor 2008, Brooks 2013). In our study, in both years, fish at younger ages were more likely to skip-spawning; skip-spawning fish ranged in age from 4 to 22. However, the highest sample sizes were from ages 2 to 16 (82% of samples in 2015 were less than 17 years old and 94% in 2011). There were significant relationships between age and skip-spawning rates, although, the annual trends were divergent; in 2011 there was a positive relationship and for 2011 and 2015 combined there was a negative relationship. These results indicate that the age effect on skip-spawning may vary and that annual data may be required to accurately model this effect. An evaluation of methods for incorporating skip-spawning into population models should incorporate potential relationships between age and skip-spawning.

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TABLES and FIGURES

Table 1. -- Number of female sablefish sampled in 2011 and in 2015 by haul and habitat or area (inshore bay, continental slope, cross-shelf gully, gully mouth, or Shelikof Strait). The % mature includes skip-spawning fish. In 2011 there were 41 hauls and in 2015 there were 18 hauls.

	2011			2015		
Haul	N	% mature	Habitat	N	% mature	Habitat
1	4	50%	Slope	0		Gully
2	4	100%	Slope	3	0%	Gully
3	26	92%	Slope	1	0%	Gully
4	39	92%	Slope	101	71%	Gully mouth
5	0		Shelf	38	86%	Gully mouth
6	0		Shelf	38	84%	Slope
7	8	13%	Shelf	29	28%	Slope
8	99	0%	Shelf	9	89%	Slope
9	20	0%	Shelf	0		Slope
10	28	4%	Shelf	18	11%	Slope
11	31	0%	Shelf	4	0%	Slope
12	6	0%	Shelf	14	33%	Slope
13	1	100%	Shelf	20	37%	Slope
14	0		Gully	42	49%	Slope
15	0		Gully	8	63%	Slope
16	3	0%	Shelf	18	56%	Slope
17	1	0%	Shelf	28	36%	Slope
18	5	80%	Shelf	113	77%	Slope
19	1	0%	Shelf			
20	22	50%	Gully			
21	17	35%	Gully			
22	7	43%	Gully			
23	6	33%	Gully			
24	21	33%	Gully			
25	26	15%	Gully			
26	0		Gully			
27	3	33%	Gully			
28	0		Shelikof			
29	0		Shelikof			
30	2	50%	Shelikof			
31	1	0%	Shelikof			
32	2	0%	Shelikof			
33	1	0%	Bay			
34	0		Bay			
35	0		Bay			
36	0		Bay			
37	3	67%	Bay			
38	1	0%	Bay			
39	5	0%	Bay			
40	0		Bay			
41	0		Bay			

Table 2. -- Number of female sablefish sampled in 2011 and in 2015 by age as well as the number of fish that were skip-spawning (“Skip”) or spawning capable (fish that would spawn that year or were skip-spawning).

	2011			2015		
Age	Samples	Spawning capable	Skip	Samples	Spawning capable	Skip
2	29			19	0	
3	154			19	0	
4	59	3	1	37	6	1
5	24	3		41	6	
6	13	6	3	39	5	
7	16	11	3	47	23	3
8	5	5	1	32	22	
9	5	4		17	13	
10	10	7	2	23	21	1
11	10	10	3	22	20	2
12	4	4	2	15	15	2
13	8	8	1	19	19	2
14	14	14	4	16	16	2
15	7	7	1	18	18	2
16	6	6	1	23	23	
17	2	2	1	10	10	
18	2	1		9	9	
19	2	2		12	12	
20	2	2		6	6	
21	2	2		4	4	
22	2	2		4	4	1
23	1	1		3	3	
24	1	1		2	2	
25	2	2		7	6	
26–30	3	3		12	12	
31–39	2	2		12	12	
40+	2	2		5	5	

Table 3. -- Linear regression parameters for relative fecundity (eggs per gram of fish weight) and age for samples collected in 2011, 2015, both years pooled. The “% decrease age 5 to 40” is the estimated decrease in relative fecundity from age 5 to 40. There is no estimate for 2011 because there was no significant trend (high “P-value slope”).

Year	Intercept	Slope (SE)	P-value slope	R^2	% decrease age 5 to 40
2011	114.89	-0.51 (0.46)	0.27	0.03	-
2015	107.60	-0.63 (0.37)	0.09	0.07	21%
Pooled	112.89	-0.66 (0.29)	0.03	0.06	21%

Table 4. -- Slope and age-at-50% maturity ($a_{50\%}$) determined from logistic models of age-at-maturity. Fish that would skip-spawning (SS) were categorized as either immature (Imm) or mature (Mat). Results for 2011 are from Rodgveller et al. (2016).

Year	SS	$a_{50\%}$	Slope
2011	Imm	9.84	0.56
2011	Mat	6.79	1.17
2015	Imm	7.94	0.67
2015	Mat	7.27	0.89

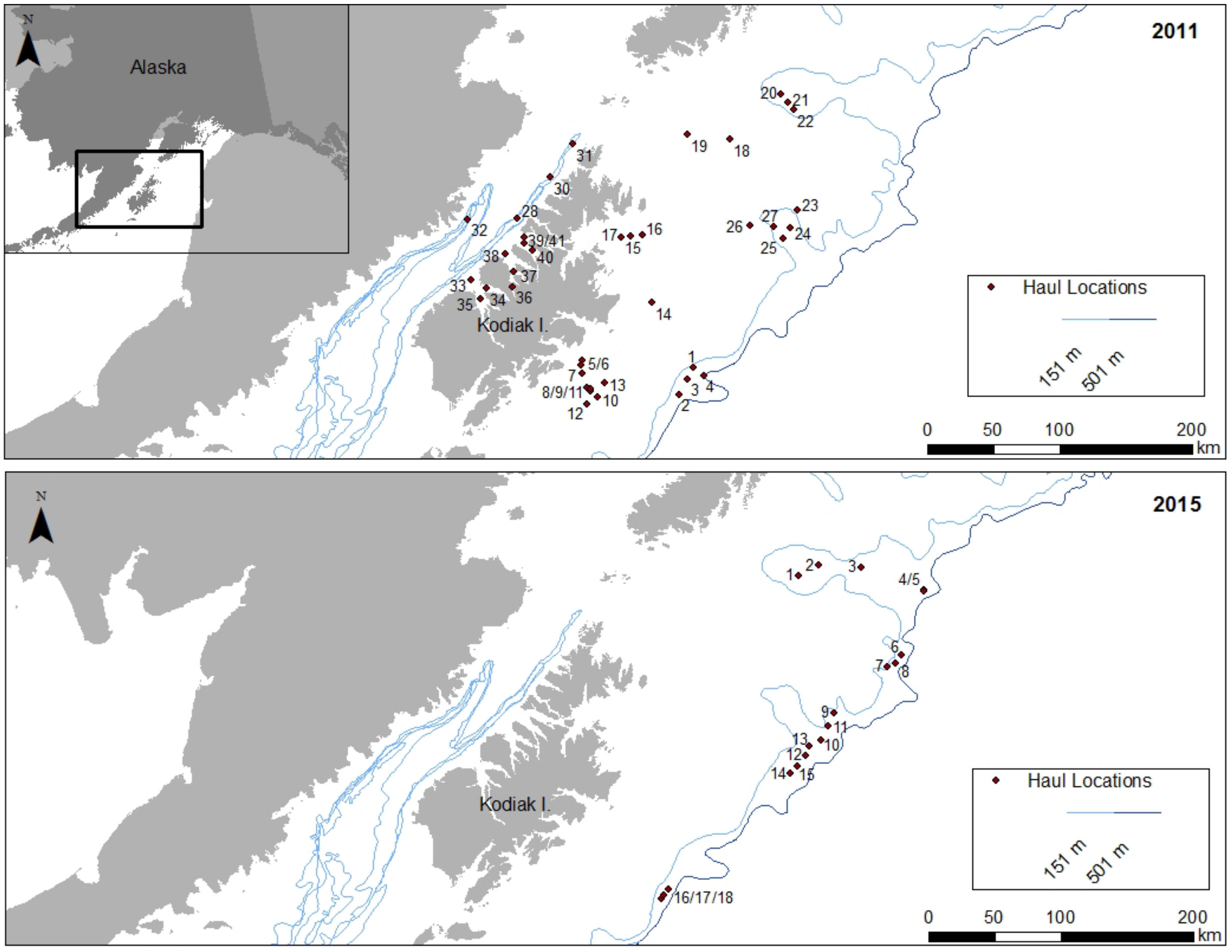

Fig. 1. -- Haul locations in December 2011 (top) and 2015 (bottom) nearby Kodiak Island (Kodiak I.) in the Gulf of Alaska.

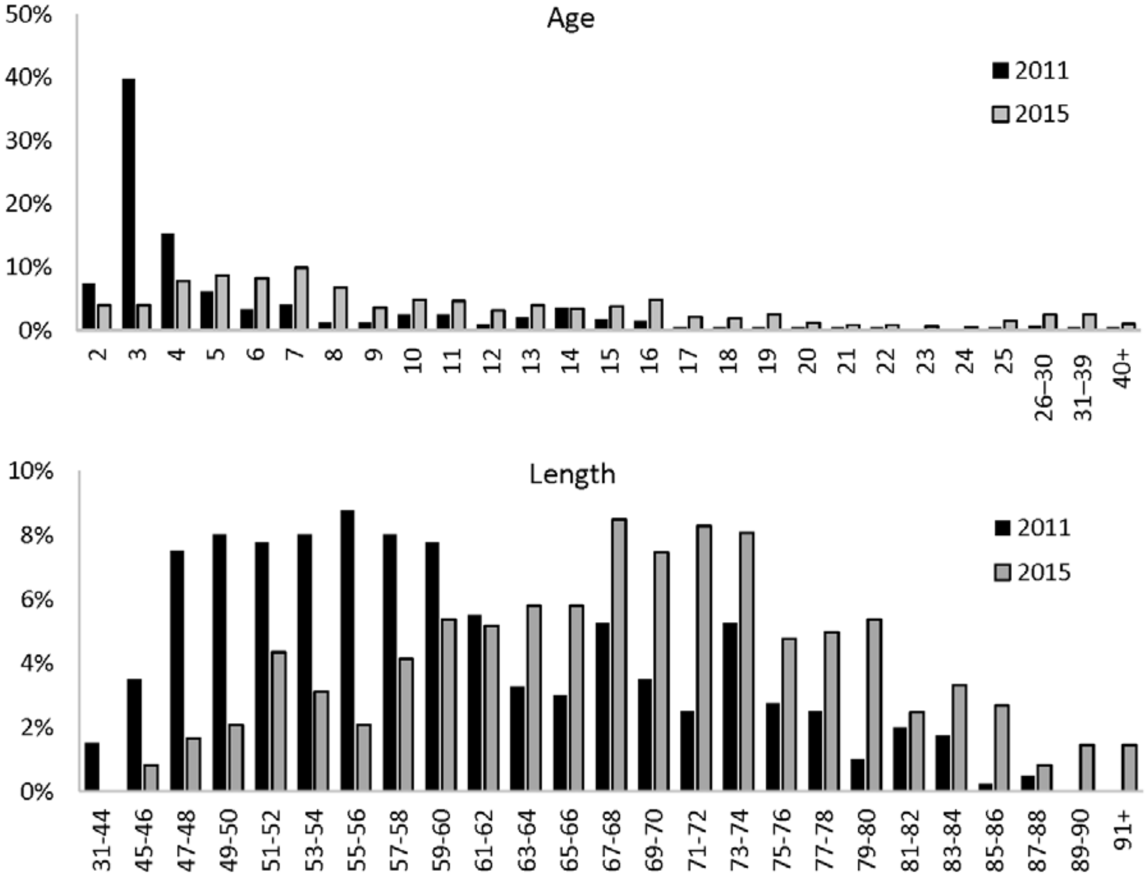

Fig. 2. -- Proportion of female sablefish at each age and length (2-cm intervals) sampled for maturity in 2011 and 2015.

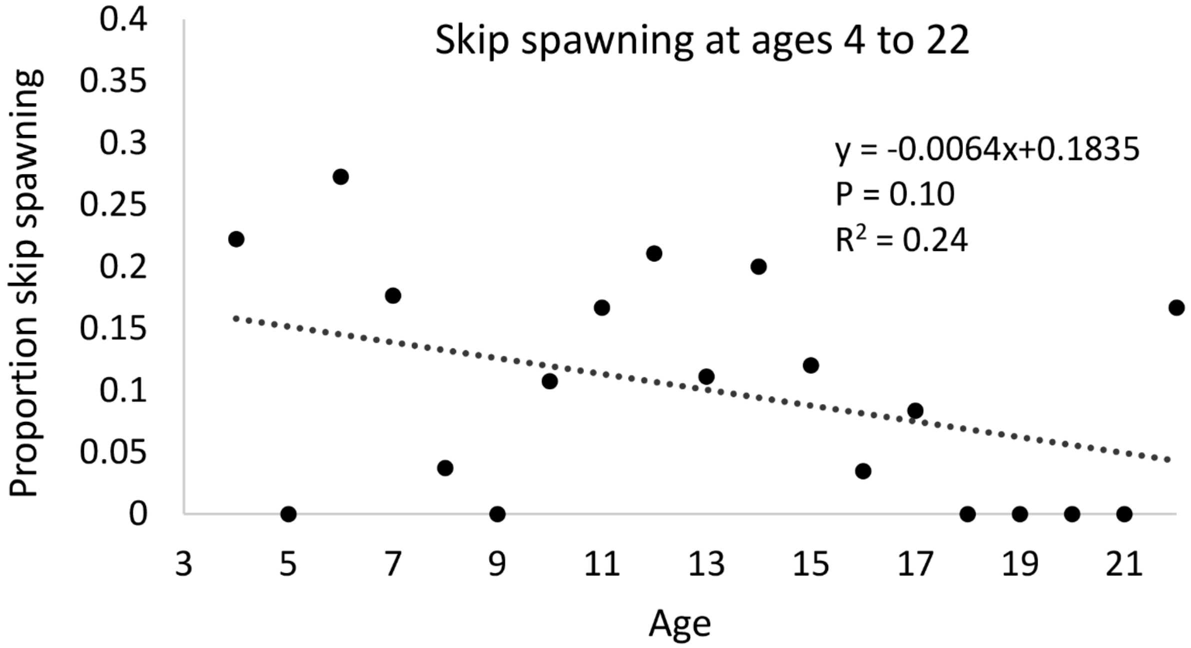

Fig. 3. -- Proportion of spawning capable fish (those that will spawn or have spawned in the past) that skipped spawning in 2011 and 2015 combined.

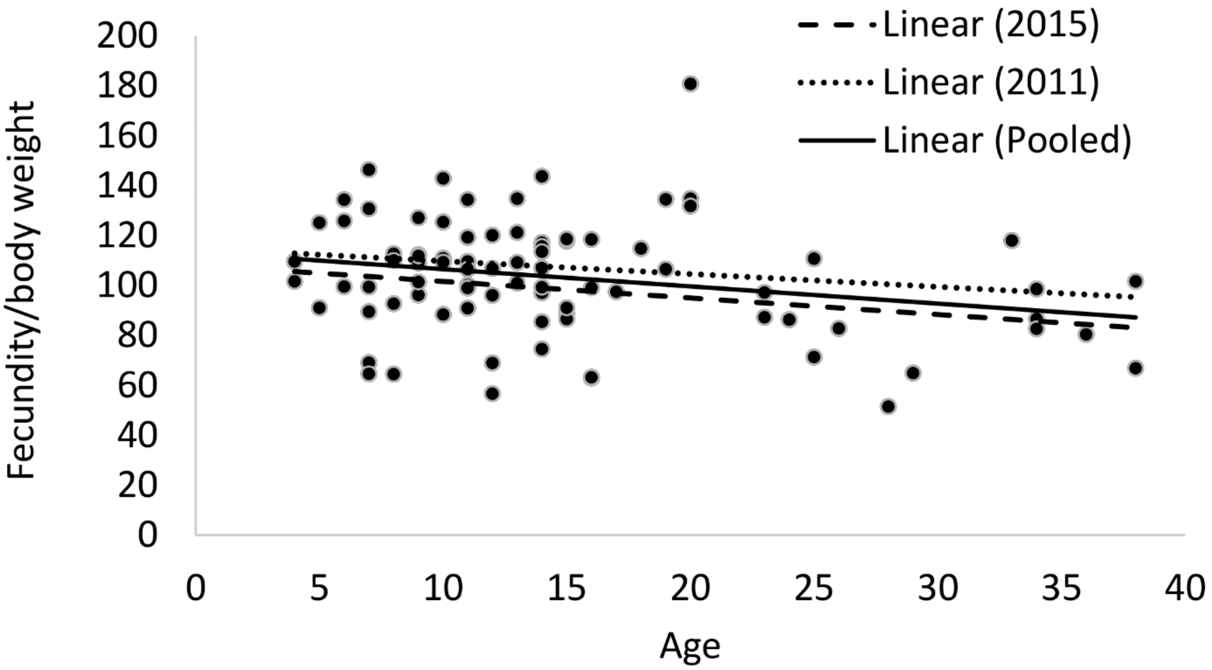

Fig. 4. -- Linear regression of relative fecundity (eggs per gram of fish weight) and age for samples collected in 2011, 2015, and both years pooled.

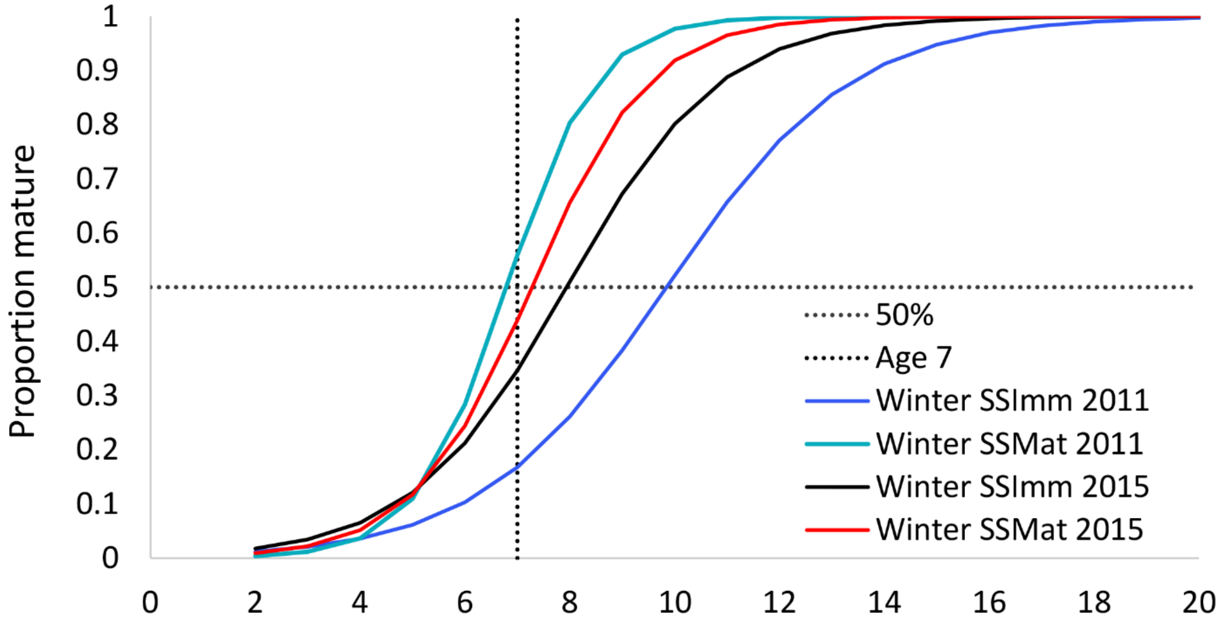

Fig. 5. -- Logistic age-at-maturity curves for female sablefish collected in either 2011 or 2015. Skip-spawning fish were either classified as immature (SSImm) or mature (SSMat). The 50% horizontal line and the vertical age 7 line are provided as references.

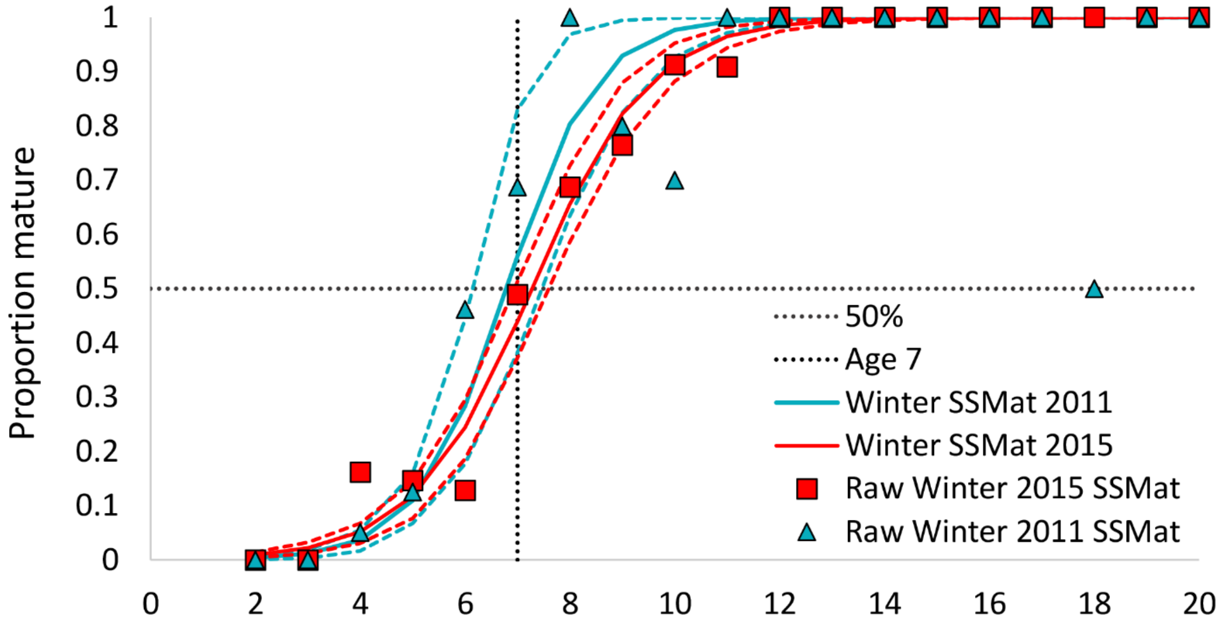

Fig. 6. -- Logistic age-at-maturity curves for female sablefish collected in either 2011 or 2015. Skip-spawning fish were classified as mature (SSMat). The 50% horizontal line and the vertical age 7 line are provided as references. Dashed lines are 95% upper and lower confidence intervals.

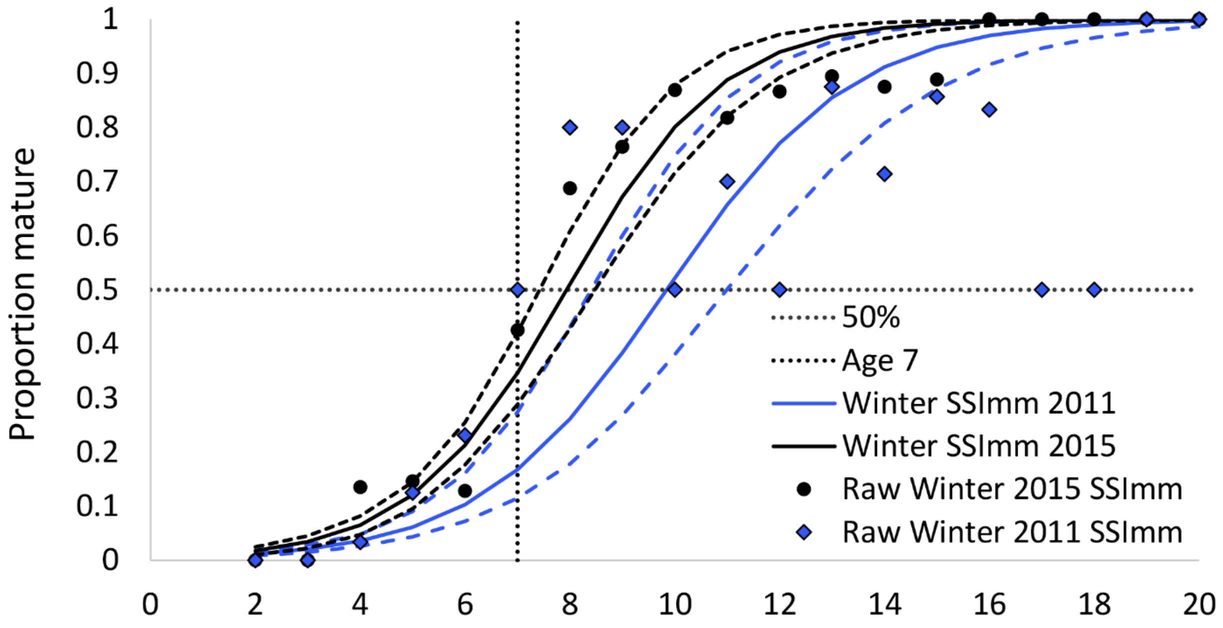

Fig. 7. -- Logistic age-at-maturity curves for female sablefish collected in either 2011 or 2015. Skip-spawning fish were classified as immature (SSImm). The 50% horizontal line and the vertical age 7 line are provided as references. Dashed lines are 95% upper and lower confidence intervals.

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